Evolution of cooperation by multilevel selection

Arne Traulsen and Martin A. Nowak*

Program for Evolutionary Dynamics, Departments of Organismic and Evolutionary Biology and Mathematics, Harvard University, Cambridge, MA 02138

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We propose a minimalist stochastic model of multilevel (or group) selection. A population is subdivided into groups. Individuals interact with other members of the group in an evolutionary game that determines their fitness. Individuals reproduce, and offspring are added to the same group. If a group reaches a certain size, it can split into two. Faster reproducing individuals lead to larger groups that split more often. In our model, higher-level selection emerges as a byproduct of individual reproduction and population structure. We derive a fundamental condition for the evolution of cooperation by group selection: if $b/c > 1 + n/m$, then group selection favors cooperation. The parameters b and c denote the benefit and cost of the altruistic act, whereas n and m denote the maximum group size and the number of groups. The model can be extended to more than two levels of selection and to include migration.

finite populations | prisoner's dilemma | group selection | fixation probability | stochastic process

Competition between groups can lead to selection of cooperative behavior. This idea can be traced back to Charles Darwin, who wrote in 1871: "There can be no doubt that a tribe including many members who..were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over other tribes; and this would be natural selection" (1). The first mathematical model of group selection was proposed in 1945 by Sewall Wright (2). The enthusiastic attempt of early group selectionists to understand all of the evolution of altruism from this one perspective (3, 4) has led to vigorous criticism and a general denial of such ideas for decades (5–8). Only a small number of biologists continued to work in this area (9–19). Over many years, D. S. Wilson was the main proponent of the idea of group selection (20–22). Nowadays, there seems to be a renewed interest in the subject, as demonstrated by many empirical and theoretical studies (23–28). The current analysis of group selection is also closely related to the attempt at understanding the simultaneous effect of natural selection on multiple-levels (29–31). In our opinion, group selection is an important organizing principle that permeates evolutionary processes from the emergence of the first cells to eusociality and the economics of nations.

Consider a population that is subdivided into groups. The fitness of individuals is determined by the payoff from an evolutionary game. Interactions occur between members of the same group. We model stochastic evolutionary dynamics. In any one time step, a single individual from the entire population is chosen for reproduction with a probability proportional to its fitness. The offspring is added to the same group. If the group reaches a critical size, n, it will divide into two groups with probability q. The members of the group are randomly distributed over the two daughter groups, see Fig. 1. With probability $1-q$, the group does not divide, but a random individual of the group is eliminated. Therefore, n resembles the maximum number of individuals in a single group. The total number of groups is constant and given by m; whenever a group divides, another group is eliminated. These assumptions ensure that the total population size is constrained between a lower bound, m, and an upper bound, mn.

Our simple model has some interesting features. The entire evolutionary dynamics are driven by individual fitness. Only individuals are assigned payoff values. Only individuals reproduce. Groups can stay together or split (divide) when reaching a certain size. Groups that contain fitter individuals reach the critical size faster and, therefore, split more often. This concept leads to selection among groups, although only individuals reproduce. The higher-level selection emerges from lower-level reproduction. Remarkably, the two levels of selection can oppose each other.

Any evolutionary game can be analyzed in our framework, but here, we focus on the interaction between cooperators and defectors. Cooperators pay a cost, c, which ensures that other members of the same group receive a benefit, b. Defectors pay no cost and provide no benefit. Defectors benefit from cooperators that are present in the same group. In any mixed group, defectors have a higher payoff than cooperators. In homogeneous groups, however, cooperators have a higher payoff than defectors. This tension might allow for the evolution of cooperation. Our aim is to calculate the associated fixation probabilities. Therefore, we study the effect of population structure on pure selection dynamics.

Imagine that a single cooperator is added to a population of defectors. What is the probability, ρ_C, that this cooperator gives rise to a lineage that replaces all defectors and takes over the entire population? As long as the cooperators exist in mixed groups, the odds are against them, but, if by chance, a homogeneous cooperator group arises, then the emerging higher-level selection works for them. Conversely we can also calculate the fixation probability, ρ_D, of a single defector that is added to a population of cooperators. Here, the situation is reversed. The invading defectors are initially favored by individual selection in mixed groups but, later, opposed by the emerging higher-level selection among homogeneous groups. We argue that selection favors cooperation if the fixation probability ρ_C is greater than the inverse of the population size, which is greater than ρ_D.

In general, even our very simple model is too complicated to allow an exact calculation of the fixation probabilities. We can make progress, however, by assuming that splitting of groups occurs only very rarely (small q). Then, most groups are at their maximum carrying capacity and consist of only cooperators or only defectors when they split. Therefore, the fixation probability is simply the product of the fixation probability of a single individual in a group times the fixation probability of this group in the population. In this limit, the model becomes a hierarchy of two Moran processes, one for individuals and one for groups. A similar setup was studied by Paulsson (31) in the context of plasmid replication in bacteria.

For the fixation probability of one cooperator in a group of $n-1$ defectors, we obtain $\phi_C = [1/n]\cdot[1 - (b + cn - c)w/2]$. For the fixation probability of one cooperator group in a population of $m-1$ defector groups, we obtain $\Phi_C = [1/m]\cdot[1 + (b - c)(m - 1)w/2]$. The intensity of selection is given by the

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*To whom correspondence should be addressed. E-mail: martin_nowak@harvard.edu.

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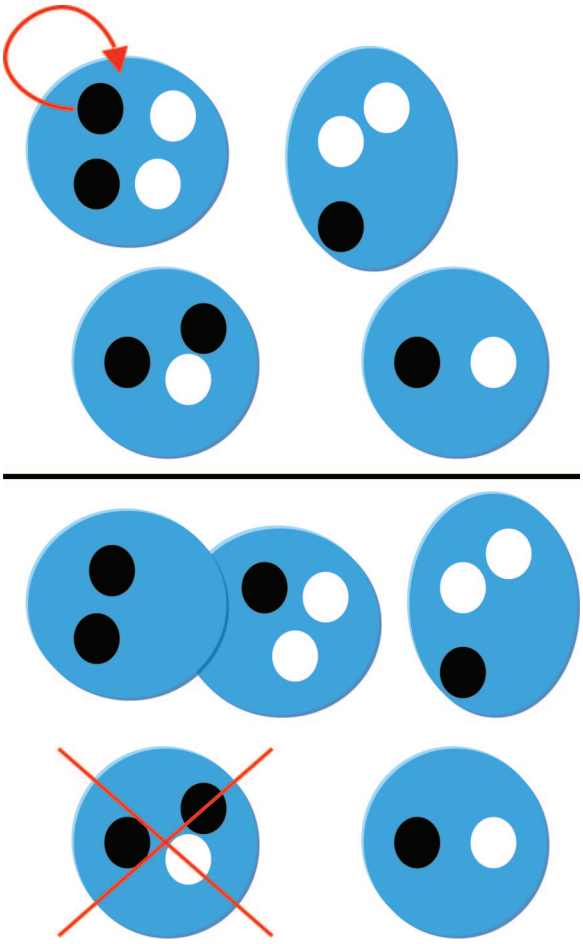

Fig. 1. The population is subdivided into m groups. Individuals interact within a group in terms of an evolutionary game. The payoff of the game is interpreted as fitness. At each time step, an individual from the entire population is chosen for reproduction proportional to fitness. The offspring is added to the same group. If a group reaches the maximum size, n, then it splits with probability q. In this case, the individuals of the group are randomly assigned to the two daughter groups, and another randomly chosen group is eliminated (to maintain a constant number of groups). With probability $1 - q$, a randomly chosen individual from the groups is eliminated. Although only individuals reproduce, there are two levels of selection. At the lower level, individuals compete with others in the same group. At the higher level, groups compete with each other; groups that contain fitter individuals have more reproductive events and, therefore, split more often. This dynamic population structure favors the evolution of cooperation if the benefit-to-cost ratio of the altruistic act exceeds 1 plus the ratio of group size divided by the number of groups: $b/c > 1 + (n/m)$.

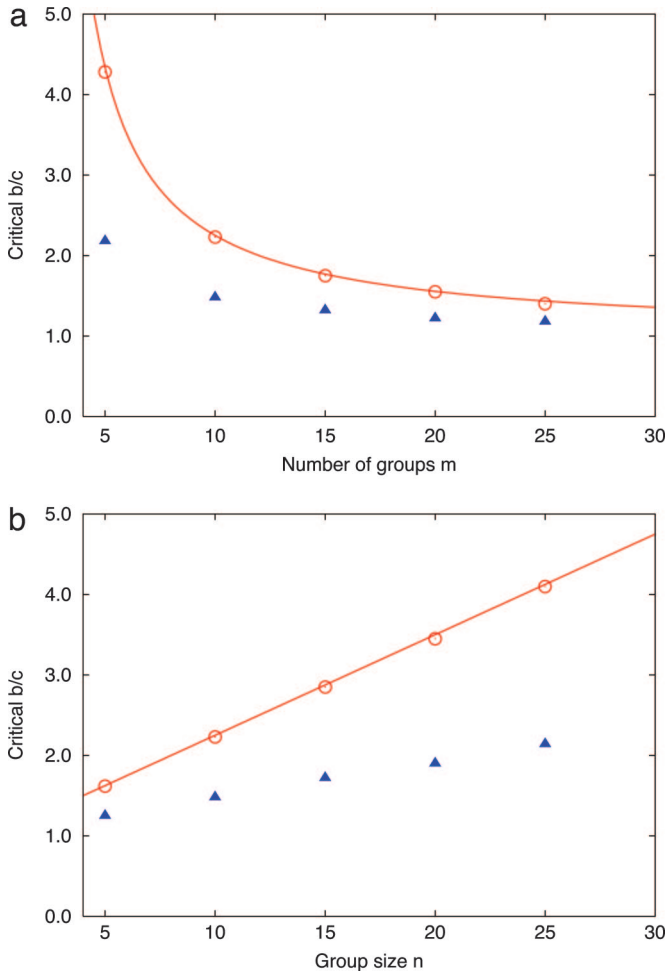

Fig. 2. The critical benefit-to-cost ratio, b/c, for which cooperators and defectors fixate with the same probability is shown for a fixed group size, $n = 10$ (*a*) and for a fixed number of groups, $m = 10$ (*b*). The numerical simulations for $q = 10^{-3}$ (circles) agree perfectly with the theory for weak selection and $q \ll 1$ given by $b/c > 1 + n/(m - 2)$; see Eq. **24** in *Supporting Text*. Simulations for $q = 1.0$ (triangles) show that the critical b/c is even smaller when q is larger: More frequent group splitting favors cooperators. All simulations are performed for weak selection, $w = 0.1$.

parameter w. Both results hold for weak selection (small w). Note that the lower-level selection within a group is frequency-dependent and opposes cooperators, whereas the higher-level selection between groups is constant and favors cooperators.

In the case of rare group splitting, the fixation probability of a single cooperator in the entire population, is given by the product $\rho_C = \Phi_C \phi_C$. It is easy to see that $\rho_C > 1/(nm)$ leads to $b/c > 1 + [n/(m - 2)]$. If this inequality holds, then cooperators are advantageous once both levels of selection are combined. In *Supporting Text*, which is published as supporting information on the PNAS web site, we also show that the same condition implies that defectors are disadvantageous once both levels of selection are combined. We note that at least $m = 3$ groups are needed for cooperation to have any chance (see Fig. 4, which is published as supporting information on the PNAS web site).

For a large number of groups, $m \gg 1$, we obtain the simplified condition

$$\frac{b}{c} > 1 + \frac{n}{m}. \qquad [1]$$

The benefit-to-cost ratio of the altruistic act must exceed one plus the ratio of group size over number of groups. This condition is intuitively appealing: Smaller group sizes and larger numbers of groups favor cooperators. In the limit $m \gg n$, all we need is $b > c$, which is the basic requirement for evolution of any altruistic behavior.

Fig. 2 demonstrates the perfect agreement between our calculation and numerical simulations for small splitting probability, q. The simulations are also performed for $q = 1$, which means that groups always split once they reach the maximum size. Larger q favors cooperators, because splitting of mixed groups can occasionally lead to homogeneous cooperator groups. Therefore, Eq. **1** is pessimistic. For larger q, even smaller values of b/c are enough to favor the evolution of cooperation. In particular, we also observe that, for larger q, already $m = 2$ groups can be enough to favor cooperation.

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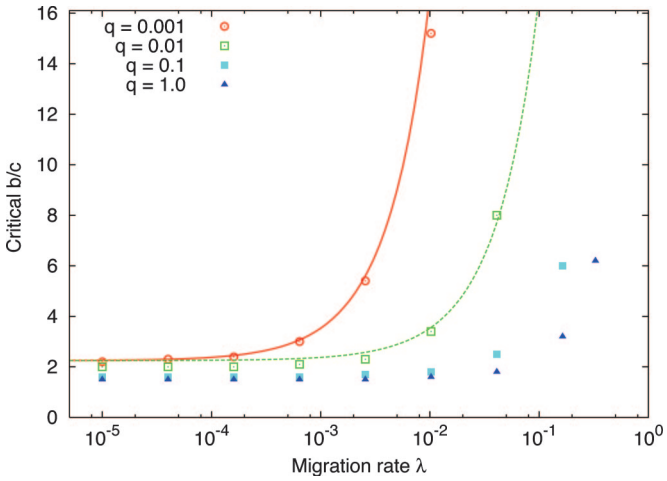

Fig. 3. The critical benefit-to-cost ratio, b/c, where cooperators and defectors have the same fixation probability, is shown as a function of the migration rate λ. After each reproductive event, the offspring can move to another group (with probability λ) or stay in the same group (with probability $1 - \lambda$). The simulations for $q = 10^{-3}$ (open circles) and $q = 10^{-2}$ (filled squares) agree well with the theory (shown as solid and dashed lines, respectively) for weak selection, $w \ll 1$, and small splitting probabilities, $q \ll 1$, given by $b/c > 1 + (n + m{\cdot}z)/(m - 2 - z/n)$; see Eq. **34** in *Supporting Text*. Simulations for $q = 1$ show that cooperators can be favored even for higher migration rates if groups split rapidly (parameters: $m = 10$, $n = 10$, $w = 0.1$).

We can relax the assumption that groups represent perfect boundaries and allow for some migration of individuals between groups. Migration can be seen as "noise" of group selection. At any one time step, there is a (small) probability, λ, that a random individual moves to another group. Migration enables defectors to invade and take over groups of cooperators. The reverse is also possible but less likely. Including migration, cooperators are favored over defectors provided

$$\frac{b}{c} > 1 + z + \frac{n}{m}. \qquad [2]$$

The benefit-to-cost ratio has to exceed the same term as before plus the average number of migrants $z = \lambda/q$ arising from one group during its lifetime. (The lifetime of a group is defined as the time between the foundation of the group and its elimination caused by the splitting of another group.) Again, Eq. **2** holds in the limit of weak selection, $w \ll 1$, and rare group splitting, $q \ll 1$. We have also assumed that $m \gg 1$; the condition for any m is shown in *Supporting Text*. For $m \gg n$, Eq. **2** means that the benefit-to-cost ratio must exceed one plus the average number of migrants arising from one group. Fig. 3 again illustrates the excellent agreement between our theory and numerical data from computer simulations.

We can extend our analysis to more than two levels of selection. On the lowest level, there is frequency-dependent selection between cooperators and defectors. On all higher levels, there is constant selection between groups, groups of groups (metagroups), and so on. If there are h levels of selection with population sizes $m_1, \ldots, m_h$, then we find that a single cooperator is an advantageous mutant if

$$\frac{b}{c} > 1 + \frac{m_1}{-h + \sum_{i=2}^{h} m_i}. \qquad [3]$$

This result holds for weak selection on all levels and ignoring migration. For $h = 2$, we recover our earlier finding. Note that Eq. **3** implies, for example, that $h = 2$ levels of selection with $m_2 = 6$ groups have the same effect as $h = 3$ levels of selection with $m_2 = 3$ groups and $m_3 = 4$ metagroups.

There is a long-standing tradition of comparing group selection with kin selection (7, 29, 30, 32–39), and, often, the distinction between these two approaches is blurred. Our present model can be interpreted as describing purely cultural evolution: Groups consist of genetically unrelated individuals, and successful groups attract new individuals, which learn the strategies of others in the same group. For this interpretation, kin selection seems to be inappropriate. But our model can also be interpreted as describing genetic evolution, in which case, the members of the same group could be said to be more related than members of different groups, and the machinery of kin selection might apply. It would be interesting to see how the mathematical methods of kin selection can be used to derive our central results given by Eqs. **1–3** and what assumptions are needed for such a derivation. The problem is that the typical methods of kin selection are based on traditional considerations of evolutionary stability, which are not decisive for games in finite populations (40).

In summary, we have presented a minimalist model of multilevel selection that allows the analytic calculation of a critical benefit-to-cost ratio of the altruistic act required for the evolution of cooperation. If $b/c > 1 + n/m$, then a single cooperator has a fixation probability that is greater than the inverse of the population size, and a single defector has a fixation probability that is less than the inverse of the population size. Hence, this simple condition ensures that selection favors cooperators and opposes defectors. The condition holds in the limit of weak selection and rare group splitting. The parameters n and m denote the maximum group size and the number of groups. If we include migration, the fundamental condition becomes $b/c > 1 + z + n/m$, where z is the average number of migrants arising from one group during its lifetime. These simple conditions have to hold for the group selection of altruistic behavior.

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